STATENS VÄXTSKYDDSANSTALT
MEDDELANDE Nr 65

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ON THE STRUCTURE OF THE CYST WALL IN FOUR SPECIES OF *HETERODERA* SCHMIDT

by

WOLFGANG WIESER

Svensk sammanfattning

STOCKHOLM 1953

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Introduction.

The present communication is the result of an investigation undertaken in connection with a scheme of soil analyses at the Branch Station at Alnarp of the Swedish Plant Protection Institute. The main object of this scheme was to study the cysts of several species of *Heterodera,* especially *H. avenae* and *H. schachtii,* in order to find out whether they can be distinguished on the basis of purely morphological facts. This explains why almost exclusively cysts from soil and not from roots of the host-plants were examined (only in *H. avenae* some cysts from the roots of oat were studied without finding decisive differences from that of the soil samples). Cysts of the following species were examined:
H. göttingiana from the Netherlands (Wageningen). *H. schachtii* from Sweden (Province Skåne), the Netherlands (Wageningen), and England (Rothamsted). *H. avenae* (= maior) from Sweden (Province Halland), the Netherlands (Wageningen), and England (Rothamsted). *H. rostochiensis* from Sweden (Province Skåne) and the Netherlands (Wageningen).[1] For examination of the surface patterns cysts were dissected and pieces of the cuticle were mounted in glycerine-jelly. The layering of the cuticle was studied in unstained sections, 15 to 20 μ thick, obtained by means of a freezing microtome. Of each species 5 to 15 cysts from each locality were examined. The least number of cysts was available in *H. göttingiana.*

Although a short account of the structure of the cyst wall of species of *Heterodera* has been given by Franklin (1939) it was felt necessary to supply a more detailed morphological description. This should serve both as a basis for further investigations into the differences between species of *Heterodera,* and as a contribution towards our knowledge of the structure of the cuticle of nematodes in general (cf. Chitwood and Chitwood 1950).

General construction of the cuticle of Heterodera.

The existence of two cuticular layers has been pointed out by Chatin (1888) in adult females, and by Franklin (1939) in cysts. This is evidently right though these two layers are composed of several other distinct layers.

[1]) I gratefully acknowledge the help of the director of the Branch Station at Alnarp, J. Mühlow, who provided me with all facilities for my work. Furthermore, I am indebted to Dr. B. G. Peters of the Rothamsted Experimental Station, and to Dr. M. Oostenbrink of the "Plantenziektenkundige Dienst", Wageningen, Netherlands, for supplying me with cysts from their respective countries.

If splitting of the cuticle occurs during sectioning this takes place always between "exo"- and "endo-cuticle" and not between some other layers of either of them. The more detailed morphology of these layers has not been discussed in species of *Heterodera* though recently Chitwood (1951) figured the cross-section of a part of the cyst wall of *H. rostochiensis* showing a schema which essentially agrees with my own observations (cf. fig. 11).

The presence of an endocuticle and an exocuticle is perhaps a common feature in all nematodes though in some cases a uniform composition of 9 or 10 layers has been described (*Ascaris, Dioctophyma renale*) without emphasizing a gross division into two main layers. In free living nematodes, at any rate, the occurrence of endo- and exocuticle is a characteristic feature.

The layering of *H. avenae* is figured schematically in fig. 1, and the following framework for a discussion of the separate components is adopted:

A.) Exocuticle
  1.) Cortical layer with surface patterns
  2.) Inner layers
B.) Endocuticle
C.) Channels and pores

If we compare fig. 1 with the representation of the cuticular layering in some other nematodes we find strong similarities with the cuticle of *Enoplus communis* as depicted by De Man (1886), if we presume that the lamella between the two "matrix"-layers (as called by Chitwood and Chitwood) actually represents the lamella between exo- and endocuticle. Also the resemblance of the cuticle of *Heterodera* to that of Ascaris lumbricoides (van Bömmel 1895) is fairly close. Less agreement exists with the cuticle of *Spilophorella* and *Dorylaimopsis* (Chitwood and Chitwood) in which the layering is fairly reduced, or with that of *Dioctophyma renale* in which it is especially developed. Finally, a word should be said on the pigmentation of the cuticle in general though it has not been made the object of close investigation. *H. göttingiana* and *H. schachtii* are less pigmentated than *H. avenae* and *H. rostochiensis*, and this difference in colour can be a means by which to distinguish between these two groups of species. (cf. also Oostenbrink in "Proceedings of the International Nematology Symposium ... 1952). However, in order to use the degree of pigmentation as a distinguishing character care has to be taken to separate small cysts from large ones since the pigmentation not only is a specific, but also an age, characteristic. In *H. schachtii* and *avenae* I usually separated cysts smaller and larger than 670 μ. The cystwall is not homogeneously pigmentated but of speckled appearance with darker and paler patches. There are two very small areas around the vulva and head where the exocuticle is not pigmentated though the endocuticle may be strongly coloured (fig. 2).

A.) Exocuticle

1.) *Cortical layer*

The most conspicuous feature of the cortical layer if examined in surface view is an irregular network of lines, the "reticulate pattern". The more or less parallel arrangement of this network in small cysts (fig. 3), and in lager cysts at the anterior and posterior ends, supports FRANKLIN's assumption that it may be derived from the cuticular annulation in the larvae. In very large cysts there is a tendency towards obliteration of the reticulate pattern, but, if well developed, it consists of discontinous ridges separated by continuous "valleys" (fig. 4). Now, either of these two components may possess a sharp, well-defined edge whereas the edge of the other one is flat and rather ill-defined, i.e. in examining a piece of the cuticle either a *discontinuous* system of lines (fig. 5) or a *continuous* network (fig. 6) is to be seen in sharp outline while the corresponding pattern possesses more blurred contours. Never are both components of the surface pattern visible with the same sharpness.

It is a curious fact that the occurrence of a distinctly outlined continuous network appears to have taxonomical value in distinguishing between different species of *Heterodera*. I observed the presence of sharply outlined discontinuous patterns in all 4 species examined but the continuous network was sharp in *göttingiana* and in *schachtii* only. Actually, there is a series beginning with *göttingiana* in which the continuous network occurs abundantly and is well developed (fig. 7), through *schachtii* with the network occurring less abundantly and being more feebly developed, to *avenae* and *rostochiensis* in which the network does not occur at all. In the latter species there is a tendency for the ridges to run in parallel lines (cf. FRANKLIN loc. cit. fig. 14/3). This tendency — but to a much lesser degree — exists also in *avenae*. In the other two species it is only around the anterior and posterior ends of the body that the ridges are arranged in parallel lines. Naturally, the analysis of the structure of the cortical layer is hampered somewhat by the darker pigmentation and more pronounced development of the punctations in *avenae* and *rostochiensis* which render the reticulate pattern more indistinct than in the two other species. Further investigation should show whether the differences emphasized above are truly specific differences or whether they are due to some effect of individual variation, or difference in distinctness of the relevant structures.

2.) *Inner layers*

In figs. 8—11 the general structure of the cuticular layering in the 4 species examined is shown. Again, the 4 species display a series as to the degree of development of the layering, which will be summarized after the

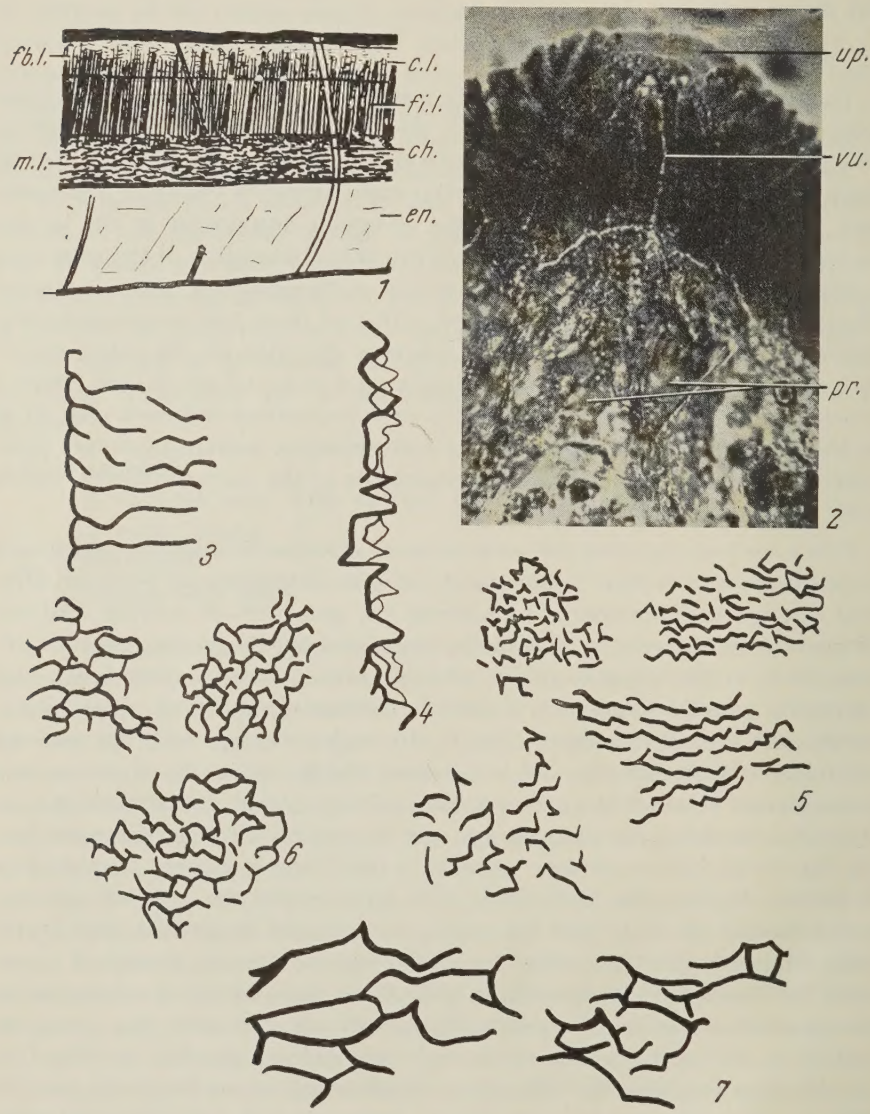


Plate 1:

Fig. 1: Schema of cuticular layering in *H. avenae*. Fig. 2: Vulvar region of *H. avenae* in median section. Fig. 3: Surface view of »reticulate pattern» of cortical layer in small cyst of *H. schachtii*. Fig. 4: Median view of »reticulate pattern» of cortical layer in *H. schachtii*. Fig. 5: The »reticulate pattern»: Schema of discontinuous system of lines in *H. avenae* and *H. schachtii*. Fig. 6: The »reticulate pattern»: Schema of continuous network in *H. schachtii*. Fig. 7: The same in *H. göttingiana*.

ch. = Channel, c.l. = Cortical layer, en. = Endo-cuticle, fb.l. = Fiber layer, fi.l. = Fibrillar layer, m.l. = Matrix layer, pr. = Projections of endo-cuticle in vulvar region, up. = unpigmented area of exocuticle around vulva, vu. = Vulva.

components of the cuticle have been discussed. The following layers of the exo-cuticle, apart from the cortical layer, can be distinguished:

Fiber layer: This is a more or less homogeneous layer, well developed in *rostochiensis* and *avenae,* indistinct in *göttingiana,* and sometimes also in *schachtii.* Its inner portion is traversed by the fibrils of the following fibrillar layer, from which it is accordingly often difficult to delimit. It is mostly somewhat paler than the cortical layer but darker than the fibrillar layer.

Fibrillar layer: This is a matrix having a heterogeneous structure and traversed by obliquely radial fibrils. These fibrils are hardly visible in *göttingiana* and *schachtii,* in cross-sections of which they only appear as the faintest oblique striations. In *avenae* and *rostochiensis* the fibrils are very well developed; in the former species they appear as dense lamellae in cross-sections; in the latter they are still more concentrated, and more regularly arranged, sometimes having vacuoles between them ("va" in fig. 11). These vacuoles appear to be homologous to those depicted by Goldschmidt (1905) in *Ascaris lumbricoides.* However, it should be stressed here that these vacuoles have nothing to do with the true pores or channels described below, but are the morphological expression of the well developed fibrils of the fibrillar layer in *H. rostochiensis.* The fibrils traverse proximally the inner matrix of the exo-cuticle and distally they reach — as already mentioned — into the fiber layer, but most probably not to the surface of the cuticle. This is a fact well known in other nematodes. Wherever the fibrillar layer is conspicuously developed e.g. in *Enoplus,* in the Chromadoridae, Cyatholaimidae, Comesomatidae, Trichostrongylidae etc., the fibrils do not reach to the surface of the cuticle (cf. Chitwood and Chitwood p. 38). If the cuticle is observed in toto the fibrils cause the appearance of punctations. In accordance with the different degree of development of the fibrils these punctations are conspicuous in *rostochiensis* and *avenae,* and indistinct in *schachtii* and *göttingiana.* In *rostochiensis* they tend to be arranged in more or less parallel rows (Franklin 1939, 1951). The fibrils are present also in cases in which they are imperceptible: that they can be made visible by proper preparation has been shown in *Ascaris lumbricoides.*

The fibrillar layer gives the best means at hand to distinguish between the different species of *Heterodera.* The degree of development of the fibrils renders easy the distinction between *göttingiana* and *schachtii* on the one side, and *avenae* and *rostochiensis* on the other side. In cross-sections the fibrillar layer is thicker in *avenae* and *schachtii* than in *rostochiensis.* In the former two species it is always of equal thickness or thicker than the following layer, the inner matrix, whereas in *rostochiensis* it is always thinner than the latter. The thickness in large cysts of the fiber layer and the fibrillar layer together varies in *rostochiensis* from 14 to 20 μ, in *avenae*

from 32 to 56 μ, and in *schachtii* from 24 to 32 μ. The series *göttingiana—schachtii—avenae—rostochiensis* exhibits the change of the fibrils from faint striations through lamellae to columns and vacuoles. Although the appearance of the fibrils is quite different in, say, *rostochiensis* and *göttingiana*, it must be presumed that their function is the same throughout the series. As to this function evidence has been provided by GOLDSCHMIDT (1905) and MARTINI (1912) that the fibrils in *Ascaris* are supporting structures and not "feeding channels" ("Saft-bahnen") as assumed by TOLDT (1899, 1904). It is most probable that this also holds true for *Heterodera*.

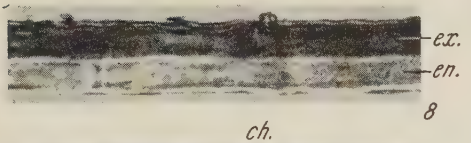
The density of the punctation, i.e. of the fibrils, varies very much in one and the same cyst. In *rostochiensis* I found from 4 to 10 punctations per μ^2. *Inner matrix*: The degree of development of this layer is closely correlated with that of the fibrillar layer, i.e. it is conspicuous in *rostochiensis* and *avenae*, more indistinct in *schachtii* (in which it is lacking in small cysts, fig. 9b); and imperceptible in *göttingiana*. As already mentioned the matrix is thicker than the fiber and fibrillar layer together in *rostochiensis* but thinner than the latter, or of equal thickness, in *avenae* and *schachtii*. It is mostly darker brown than the fibrillar layer. Its structure is somewhat heterogeneous. It is bounded internally by a *boundary layer*. The thickness in large cysts of the inner matrix is about 16 μ in *schachtii* (if present), and varies from 20 to 24 μ in *avenae*, and from about 24 to 28 μ in *rostochiensis*.

B.) *Endo-cuticle*

This is a fibrous layer of homogeneous, more or less amorphous appearance in *göttingiana, schachtii,* and *avenae*. In this respect it resembles the inner matrix in *Enoplus communis* (DE MAN 1886). Sometimes faint radial, sometimes faint circular striations can be seen. It may be darker or paler than the exocuticle.

In *rostochiensis,* however, the endo-cuticle is of quite a different appearance since it is split into a number of layers (three?) running round the cyst. This has already been observed by FRANKLIN (1939, p. 129) and resembles the condition in *Ascaris lumbricoides* in which what can be called endocuticle is divided into three "fiber-layers" (VAN BÖMMEL 1895). There the endo-cuticle is a paler brown than the exocuticle.

Plate 2:
Fig. 8—11: Sections through cyst wall, × 250. Fig. 8: *H. göttingiana.* Fig. 9a: *H. schachtii,* large cyst. Fig. 9b: *H. schachtii,* small cyst. Fig. 10: *H. avenae.* Fig. 11a, b: *H. rostochiensis,* large cyst. Fig. 11c: *H. rostochiensis,* small cyst. Fig. 12: Median section through vulvar region of *H. rostochiensis* to show cuticular projections. Fig. 13: Schema of channels in *Heterodera.* Fig. 14: »Network of pores» in *H. göttingiana,* oblique surface view. Fig. 15: »Mushroom-shaped pores» in *H. schachtii,* section, × 375.
m. = Matrix layer, va. = »Vacuoles», cu. = Cuticle, po. = Pores. For other symbols see plate 1.



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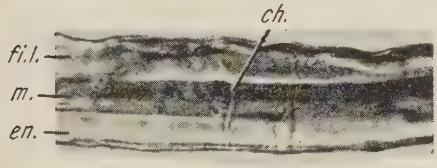

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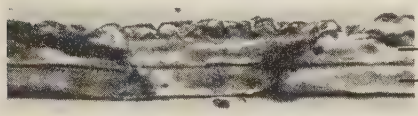

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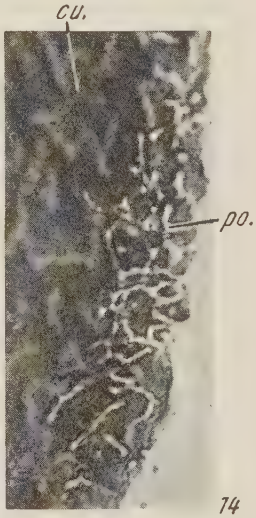

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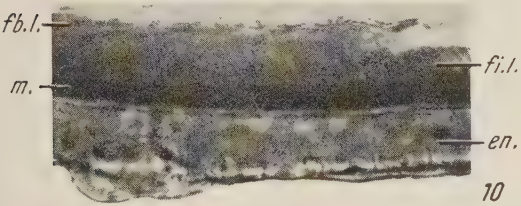

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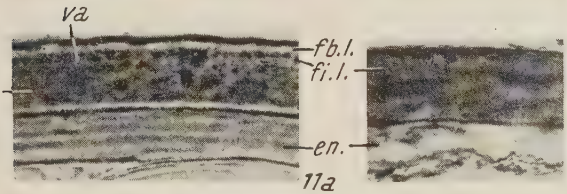

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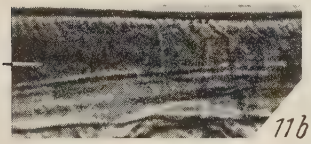

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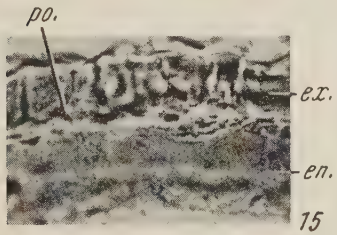

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As already observed by FRANKLIN, off-shoots and "knob-like projections" of the cuticle can be seen in the vulvar region, (figs. 2, 12). These projections are derived exclusively from the endo-cuticle. The layering of the exo-cuticle is not disturbed in this area. FRANKLIN thought that these projections "may originally have been points of attachment for muscles".

The thickness of the endo-cuticle in large cysts varies from 28 to 32 μ in *rostochiensis*, from 24 to 36 μ in *avenae*, from 20 to 28 μ in *schachtii*, and from 20 to 24 μ in *göttingiana*.

Within, the endo-cuticle is bounded by a *basal lamella* which can be more or less straight or of uneven outline.

C.) Channels and true pores

It has been shown that the structures sometimes called "pores" (= vacuoles) in *rostochiensis* actually are the expression of the well developed fibrils of the fibrillar layer of the exo-cuticle. By analogy with the facts known in other nematodes, and concluding from the structure of the same fibrils in *göttingiana*, *schachtii*, and *avenae*, it is assumed that these "pores" have no physiological function but that their origin is due to mechanical causes.

However, there exist several features to which can be ascribed the role of true pores or channels. Above all, there are conspicuous channels encountered in all species of *Heterodera* traversing the cuticle. CHATIN (1888) stated that no cuticular pores occur in adult females. FRANKLIN, however, observed these channels for the first time in cysts. She wrote on this point: "... narrow wavy lines, having the appearance of very fine channels, can be seen traversing the wall. The exact nature of these lines was not determined."

These channels occur abundantly in all *Heterodera*-species and all over the cyst, but they have a patchy distribution being more concentrated in certain areas of the cyst wall. Their average width is 2 μ. They can be simple or branched (fig. 13). Nothing is known as to their nature but the following possibilities exist and the following assumptions can be made:

1) Their origins is purely mechanical and the result of the growth processes of the cuticle of the adult female. However, the shape of the channels does not fit in with such a view.

2) They are ducts of hypodermal glands, though their being branched renders this view very improbable. Moreover, no hypodermal glands are known in phasmidian nematodes apart from amphids, phasmids, and the excretory system (cf. CHITWOOD and CHITWOOD, p. 45).

3) They represent remnants of the hypodermal protoplasm as have been described in *Ascaris megalocephala* by ROHDE (1885).

4) They are feeding channels of the cuticle, i.e. comparable with TOLDT's

"Saft-bahnen". However, they are *not* homologous with the latter since these have been proved to be the fibrils of the fibrillar layer (see above). In this connection it should be remembered that the cuticle of nematodes differs from that of arthropods not only chemically but also in being not a secretion but a sort of "connective tissue exoskeleton" which is living and growing even after the last moult (SCHNEIDER 1866). Thus the existence of feeding channels could be understandable, but no similar structures are known to occur in other nematodes.

5) The channels are connected with the diffusion of liquids or gases through the cuticle. Again, nothing similar is known in other nematodes. On the other hand, we know how important is the diffusion through the cuticle of water and root-diffusates to cause hatching of the larvae, but we do not know whether the diffusion of liquids and gases is ensured by the permeability of the cuticle alone or whether open connections with the surrounding medium may play a part in this process. The only investigation on the permeability of the cuticle of *Heterodera* is that by ELLENBY (1946 a, b) and does not supply an answer to this question. ELLENBY found that the cyst wall is permeable to water, but at the same time he showed that perforation of the cysts will cause many more larvae to hatch than will hatch from undamaged ones. In other words, there is some positive influence on the hatching rate due to an open connection with the surrounding medium. ELLENBY suggested the presence of an "inhibiting cause" in closed cysts. Now the channels described might be considered as minute perforations of the cyst wall ensuring a similar — though less conspicuous — connection with the surrounding medium to that caused by the perforations experimentally made by ELLENBY. However, the nature of these channels cannot be determined by purely morphological investigations of the cyst only. Future investigations ought to follow two trends:

1. the determination of the time, and — if possible — mode of appearance of the channels in the life-history of *Heterodera*-species,

2. the evaluation by means of experiment of the possible role of the channels in all processes in which diffusion or absorption of liquids or gases is involved.

An extraordinary feature has been encountered in single cysts of *H. göttingiana* from Holland, and in *H. schachtii* from England, which might be interpreted as a further development of the channels described above. In several regions of these cysts the cuticle is traversed by a *network of pores* (fig. 14) which actually gives these areas a spongy appearance. The "network of pores" is built up of a great number of short ducts anastomosing with each other in all directions and traversing both endo- and exocuticle. As to the possible significance of this peculiar structure I have no idea; it might be a pathological development of the normal channels or else a feature endowed with some special physiological function. At any

rate, the elaborate construction excludes its being due to the action of some predator; nor can it be accounted for by bacterial diseases.

Finally, I discovered in single cysts of *H. schachtii* from England a still more peculiar sort of pore which I should like to call *"mushroom-shaped pores"* (fig. 15). Patches of these pores are found in the exo-cuticle, the disk-like swellings situated proximally near the boundary layer. However, I am not sure whether there is not sometimes a connection in the form of narrow ducts through the endocuticle (possibly with the hypodermis in adults). My material does not allow me to make a definite statement on this point. In the cyst shown in fig. 15, no ducts through the endo-cuticle were present, but in another cyst, parts of the cuticle of which could be studied in oblique surface view only, I had the impression that such ducts through the endo-cuticle did occur. Strangely enough, I believe I have observed granular matter in the swellings of the "mushroom-shaped" pores. If this is true a secretive or excretive function must be ascribed to them, which view would also be supported by the peculiar shape of the pores.

Summary of differences between the four species of Heterodera

	göttingiana	*schachtii*	*avenae*	*rostochiensis*
Pigmentation	relatively pale		dark	
Reticulate pattern of cortical layer: distinctness	fairly distinct in all cysts		indistinct in large cysts, fairly distinct in small ones	
continuous network	very common	fairly common	absent	
Distinctness of fibrils (= punctations) of fibrillar layer	weakly developed		conspicuous without vacuoles	conspicuous with vacuoles
Matrix of exo-cuticle: distinctness	indistinct	indistinct in small cysts feebly developed in large ones	conspicuous	
thickness	—	thinner than or as thick as fiber and fibrillar layer together		thicker than fiber and fibrillar layer together
Endo-cuticle	homogeneous			split into a number of layers

Svensk sammanfattning.

I föreliggande meddelande diskuteras cystskalets morfologi hos följande arter: *Heterodera göttingiana, schachtii, avenae* och *rostochiensis*. Cystorna härröra från Sverige, England och Holland. Ytstrukturen undersöktes på helpreparat i glyceringelatin, och skiktningsstrukturen på snitt, som framställts med hjälp av en frysmikrotom.

Den vanliga uppbyggnaden av kutikulan i cystan är följande:

A.) Exokutikula
  1.) Kortikalt skikt med ytstruktur
  2.) Inre skikt
B.) Endokutikula
C.) Kanaler och porer

Denna uppbyggnad jämföres med kutikularstrukturen hos andra nematoder och härvid fastställes att principiell överensstämmelse finnes mellan såväl fritt levande former (*Enoplus communis*) som parasitära (*Ascaris*). Andra former som *Dioctophyma renale* och *Spilophorella* avvika från *Heterodera*kutikulans byggnadstyp.

De olika kutikulaskikten visa var för sig följande karakteristiska drag:

A.) Exokutikulan

1.) *Kortikala skiktet*

Dess struktur kännetecknas av ett system av upphöjningar och fördjupningar, som sannolikt kunna härledas från larvkutikulans struktur. Upphöjningarna synas som osammanhängande linjer (fig. 5) och fördjupningarna som sammanhängande fält (fig. 6). Om dessa strukturer överhuvudtaget äro tydliga, så har antingen de osammanhängande linjernas system eller de slutna fältens en skarp kant medan den andra har mera otydlig kontur. De båda strukturelementen kunna aldrig iakttagas med samma skärpa. Det tycks vara möjligt att tydligt se de slutna fälten hos *H. schachtii* och *göttingiana*, under det att hos *H. avenae* och *rostochiensis* endast systemet med de osammanhängande linjerna är tydligt.

2.) *Inre skikt*

a) Det fibrösa skiktet: Detta skikt finnes under det kortikala skiktet och är tämligen homogent. Det är väl utvecklat hos *rostochiensis* och *avenae*, mindre väl utvecklat hos *schachtii* och ännu svagare hos *göttingiana*. Dess inre delar genomkorsas av fibriller från det innanför liggande skiktet.

b) Fibrillskikt: Ett skikt med heterogen struktur som genomkorsas av diagonalt radiära fibriller. Dessa fibriller äro knappt skönjbara hos *göttingiana* och *schachtii*, men mycket välutvecklade hos *avenae* och *rostochiensis*. Hos sistnämnda art äro de mera regelbundet placerade än hos

de andra arterna, och vakuoler kunna uppträda mellan dem. Fibrillerna nå icke ut till kutikulans yta utan endast in i det fibrösa skiktet. Från ytan framträda fibrillerna som kutikulans punktering, som är otydlig hos *göttingiana* och *schachtii* men hos *avenae* och *rostochiensis* är tydligt framträdande. Fibrillerna ha mekanisk funktion och fungera icke som "Saftbahnen", så som av Toldt antagits vara fallet hos *Ascaris*. Fibrillskiktet är tunnare hos *rostochiensis* än hos de övriga arterna.

c) Inre matrix: Utformningen av detta skikt är korrelerad med utformningen av fibrillskiktet. Det har en heterogen struktur. Hos *rostochiensis* är det tjockare än hos *avenae* och *schachtii*. Hos små cystor av *schachtii* kan det saknas, hos *göttingiana* saknas det synbarligen helt. Inåt begränsas det av en *gränslamell*.

B.) Endokutikulan

Ett fibröst skikt, som synes vara tämligen homogent hos *göttingiana*, *schachtii* och *avenae*. Hos *rostochiensis* tycks det dock vara sammansatt av flera (3?) koncentriska skikt. I Vulvaregionen förekomma kutikulära bildningar och utväxter, som bildas av material från endokutikulan. Inåt begränsas det av en basallamell.

C.) Kanaler och porer

En ingående beskrivning lämnas av kanaler som hos alla *Heterodera*-arter förekomma strödda över hela kutikulan. De kunna vara enkla eller förgrenade, men visa sig som äkta kanaler, som genomlöpa hela kutikulan. Fem olika antaganden om dessa kanalers funktion omnämnas. Varje möjlighet till jämförelse med andra nematoder saknas dock. Ytterligare två strukturer omnämnas, som endast funnits i vissa enskilda cystor och blott hos vissa arter, nämligen ett nätformigt system av porer, som i vissa cystor av *H. schachtii* och *göttingiana* kunna genomlöpa kutikulan på bestämda ställen, och "svampformiga porer", som funnits i *H. schachtii* och kanske verkligen fungera som porer med exkretorisk eller sekretorisk funktion, då de tyckas fyllda med en kornig substans och dessutom äro ampullärt utvidgade vid basen. Det är inte helt klarlagt, huruvida dessa porer blott ligga i exokutikulan (fig. 15) eller om de ibland fortsätta in i endokutikulan.

Slutligen lämnas en morfologisk översikt över alla differenser i kutikulan hos de fyra undersökta arterna.

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